XXVII. *On the Anatomy and Affinities of* Pteronarcys regalis, *Newm.: with a Postscript, containing Descriptions of some American* Perlidæ, *together with Notes on their Habits. By* George Newport, *Esq., F.R.S., F.L.S. &c. &c.*

Read May 2nd, and June 20th, 1848.

THE existence of a winged insect which retains the branchial form of the respiratory organs of its larva state as a permanent structure, was looked upon by naturalists, when first announced *, as so curious a condition of life, that many doubted its reality. Indeed, when I first observed branchiæ in a specimen of *Pteronarcys regalis* (Tab. XXI. fig. 1), preserved in spirit, and brought to this country by George Barnston, Esq., from Canada, I was fain to regard them merely as of accidental occurrence, the result of incomplete development, similar to what is sometimes observed in the partial retention of branchiæ in adult *Amphibia*, an example of which has lately been shown to me in a Triton from Tunis. I was then disposed to think that the *Pteronarcys*, like this Triton, had not completed its changes; and, consequently, had retained in its imago form a structure which it possesses as a normal organ in its inferior condition as an aquatic larva, or pupa (fig. 2). But on minute examination, other parts of its body were found to be of a perfectly natural type, a fact which was strongly opposed to this view, since a well-marked aberration of form, or retardation of development in one part of a body rarely or never occurs without some alteration in another.

On comparing this specimen with others preserved in a dried state, and now in the cabinets of the British Museum, but which originally belonged to the Entomological Club, and are the type specimens from which Mr. Newman described his species, I immediately found that the retained branchiæ were not peculiar to the insect in my possession; as branchiæ, more or less developed,

* Meeting of Entomological Society, December 4, 1843, and Annals and Magazine of Natural History, January 1, 1844, p. 21.

but imperfectly preserved in the dried insect, and consequently most easily overlooked, exist in all the specimens of the different species of *Pteronarcys* in that collection. Branchiæ were thus found to be normal structures in the imago *Pteronarcys*, and even to characterize the genus, although they had hitherto entirely escaped observation.

Since the period when I obtained my single specimen, in December 1843, I have anxiously awaited the receipt of other examples of the insect preserved for dissection; but as I have not yet been so fortunate as to obtain them, and as I desire to make known some account of the internal structures of this remarkable insect, I have now made an anatomical examination of my specimen, having taken especial care to preserve it as entire as possible, in illustration of the facts of its anatomy, and in authentication of my account of them.

M. Pictet, the most diligent and elaborate of all monographers of the *Neuroptera*, has regarded the insects of the genus *Pteronarcys*, Newm.*, as only large *Perlidæ* †, which have the body strong and elongated, and the wings large and supported by numerous and solid reticulations. He has, however, very properly, retained the genus as established by Mr. Newman on the structure of the wings. But the entire organization of *Pteronarcys*,—not merely those portions of its external anatomy, the branchiæ, which were unknown to that gentleman when he established the genus, but also the whole of its internal conformation,—most fully authorise the separation of *Pteronarcys* from *Perla*. The peculiarities of the structures I am about to describe prove the correctness of view, and the acuteness of zoological perception and tact, which led the naturalist just mentioned, although entirely unacquainted with the anatomy of some of the primary and really important organs of the insect, —the peculiarities of which, doubtless, are of first importance in the life and habits of the species,—to establish his genus on characters which then were the most obvious for zoological description, although of only secondary physiological consequence,—the reticulations of the wings.

To understand rightly the nature of the peculiarities of this insect, I must

* Entomological Magazine, vol. v. p. 175.

† Histoire naturelle générale et particulière des Insectes Neuroptères. Première Monographie, Famille des Perlides. Genève, 1841, p. 126.

first mention that, like a very large proportion of the *Neuroptera*, it is entirely aquatic in its larva and pupa (fig. 2) states, and, consequently, that its respiration is then wholly branchial; but that in its imago or perfect state (fig. 1) it not only possesses true spiracles and tracheæ for atmospheric respiration, like other winged insects, but also retains the branchiæ of its earlier conditions, both on its thoracic and its abdominal segments, fitted for aquatic respiration. Now, although branchiæ invariably perform similar functions in all insects which possess them, they have hitherto been found only in the larva and pupa states. They are situated on different parts of the body in different genera, and, as naturalists are aware, exist, sometimes even in different species of the same genus, under different forms. In the true *Libellulæ* they are anal, and are contained within a cloaca or cavity posterior to the termination of the alimentary canal, into which the respired water is drawn by the insect at each inspiration, and is expelled from it in expiration. When this act takes place by a forcible effort on the part of the insect, it urges the body forwards, and thus becomes an act of progression. In the *Agrionidæ* the branchiæ consist of long caudal plates, through which the blood circulates to be submitted to aëration. In the *Ephemeridæ*, as in *Ephemera vulgata*, the branchiæ are both caudal and abdominal, each ring of the abdomen being furnished with bipectinated, projecting cilia, folded over the upper surface of the body. In the genera *Palingenia* and *Baëtis* of M. Pictet and Dr. Leach the abdominal branchiæ are both pectinated and lamellate, the lamellæ being folded upwards on the dorsal surface of the body. In *Potamanthus cinctus*, according to Pictet*, they are simply dendrical and setaceous, the setaceous terminations of the included tracheæ being the apices of the branchiæ; while in some few species of the same genus, as in *Potamanthus erythrocephalus*, they are lamellate, as they are also in *Cloë*. In the whole of the true *Phryganidæ*, *Mystacidæ*, *Trichostomes* and *Sericostomes*, the branchiæ are simple, hair-like structures, which cover the sides and dorsal surface of the abdomen, and these are retained in the pupa state as the respiratory organs. In *Rhyacophilus vulgaris*†

* Hist. nat. des Ins. Neuropt. Seconde Monogr., Fam. des Ephémérines. Genève, 1843, pl. 28. figs. 1 & 2. p. 198.

† Recherches pour servir à l'Histoire et l'Anatomie des Phryganides. Par J. F. Pictet. Genève, 4to, 1834, pl. 15. fig. 1.

the branchiæ have the same simple form, but instead of being distributed over the whole surface of the body they are collected into tufts, one on each side of each abdominal segment. In the *Hydropsyches* also they are setaceous and tufted, not merely at the sides of the abdomen, but also at the terminations of the caudal styles. In the *Sialidæ*, which come near to the *Perlidæ*, the respiration of the larva is both caudal and abdominal. Each segment of the abdomen in *Sialis* has a pair of single, articulated, lateral branchiæ projecting from it, while the caudal styles also are respiratory organs, as in *Agrion* and *Hydropsyche*.

In some of the *Perlidæ*, as in *Nemoura*, Pictet has shown * that the branchiæ are not tufted, as in *Perla*, although they are almost entirely confined, as in that genus, to the thoracic instead of the abdominal segments. They consist of single cylindrical appendages, as in *Sialis*, and project from the pectoral surface of each of the thoracic segments, three pairs from each. In the true *Perlidæ* † the branchiæ are tufted, are almost entirely thoracic, and are found in the whole of the species, except only in two or three, *Perla virescens*, *P. nigra* and *P. abnormis*, Newm., the *P. arenosa* of Pictet ‡. In all other known species the sternal surface of each thoracic segment has on each side one or more tufts of these branchial filamentous appendages. Usually each tuft is formed of three bundles or packets of these simple structures, into each of which a minute branch of a tracheal vessel is extended, and around which the blood circulates to be aërated. Pictet has shown that in the larva of *Perla bipunctata*, as also in other species, the middle one of each three tufts covers the future respiratory orifice or spiracle in the imago. A very similar form of tufted branchiæ exists in *Pteronarcys* (figs. 3 & 4).

The *Pupa* (fig. 2) of *Pteronarcys regalis*, the subject of the present communication, was discovered by Mr. Barnston, who favoured me with a specimen of it, but it has not yet been described. It differs both in its general appearance and habit from that of *Perla*. It is of a dark olive colour, and is covered with slight pubescence. The head is short and triangular, with setaceous antennæ, almost equal in number of joints to those of the imago. On the upper surface of the head there are three rudimentary ocelli, and the eyes project

* Monogr. Fam. des Perlides, pl. 53. fig. 7.

† *Loc. cit.* pl. 11. figs. 7 & 8.

‡ See Postscript to this paper.

widely from the posterior angles. The mandibles are short, strong and corneous, agreeing in structure with the carnivorous habits of the species. The palpi are much shorter than in the imago. The prothorax is quadrangular, much wider than long, with free elevated margins, and with the angles elongated and slightly curved. The rudiments of the wings are broad and flattened, the posterior pair being directed transversely outwards. The abdomen is cylindrical, slightly tapering, and formed of ten segments, with obsolete marks of spiracles at the sides. The ninth segment is exceedingly short on the ventral surface, but is much elongated, and is united with the terminal portion of the tenth, on the dorsal, projecting over, and completely covering the ventral portion of the tenth segment as a triangular process. The ventral portion of the tenth or anal segment is very short, and is divided longitudinally into two plates, which give origin to the caudal styles. The eighth segment in the male pupa has its posterior margin on the ventral surface elongated, as in the male imago. The legs are strong and powerful, and the meso- and metathoracic pairs have the tibiæ densely ciliated for swimming. The branchiæ on the pectoral surface of the thoracic segments correspond precisely, both in the situation and number of the tufts, with those of the imago, excepting only that the filaments are larger and more elongated, and one tuft exists in the pupa in the place of the future prothoracic and mesothoracic spiracles, which is wanting in the imago, in which the spiracles exist.

Branchiæ.—In the perfect insect (fig. 5) there are eight sets of branchial sacs, or tufts (*b*, *b*, *b*), distributed over the pectoral surface of the thoracic segments, and first two segments of the abdomen. The first of these is situated in the soft tegument that connects the head and prosternum. It consists of three pairs of sacs arranged transversely, and partially encircling the neck like a collar or ruff. The second set consists of two pairs of sacs, one of which is behind the coxæ of the first pair of legs, and the other immediately behind the ante-furcal orifices (*f*) in the prosternum. The third set consists also of two pairs of sacs situated on the anterior of the mesosternum. The fourth is a single pair of sacs between the coxæ of the second pair of legs and the mesofurcal orifices (*g*). The fifth set, like the third, is formed of two pairs of sacs, one of which is in the tegument that connects the meso-

and metathorax, below the second, or mesothoracic spiracles, while the other projects from the anterior of the metasternum. The sixth, like the fourth, is only a single pair of sacs in the soft membrane of the articulation of the coxæ of the third pair of legs (*h*); while the seventh and eighth, also single pairs of sacs, project from the inferior lateral surface of the first and second abdominal segments, in situations nearly corresponding to the usual place of spiracles in other insects.

M. Pictet has described the branchial tufts in the larva of *Perla bipunctata* very precisely, and has successfully combated the opinion put forth by M. Burmeister, in opposition to his view, that the branchial filaments are only stiff hairs. A careful examination of the tufts in *Pteronarcys* has confirmed to me the correctness of M. Pictet's observations as regards their true nature. Each tuft or sac (fig. 3) is an extension outwards of the soft tegument from which project an abundance of delicate cæcal filaments. Each filament (fig. 4) is a simple, unarticulated, uniform structure, slightly tapering and closed at its extremity, and in the interior of which there is an extremely minute tracheal vessel (*c*). On examining some of these filaments taken from the branchiæ of my specimen of *Pteronarcys* formerly, in company with Professor M.-Edwards, we were unable, at that time, to satisfy ourselves of their true branchial function; but longer-continued, repeated, and more carefully conducted investigations have now most fully satisfied me of their real importance as active organs in the imago. The uncertainty of former examinations arose, as I now find, from the branchial filaments being greatly altered in their appearance by the contraction of their fibrinous tissue, together with the coagulation of the circulatory fluid and blood-corpuscles within them, occasioned by the insect having been killed and preserved in spirits. I have since recognised corresponding appearances, induced by a similar cause, in the branchiæ of other insects killed in like manner.

The number of filaments produced from each sac varies from about twenty to fifty or more. It is greatest in the sacs of the meso- and metathorax, and smallest in those of the neck and of the abdomen. The filaments originate in little bundles, four or five in each, from the distal border of the sac, but not all on precisely the same line. Usually each filament is simple and distinct; but in a few instances, as in some (fig. 4) from the external sac at the anterior

of the mesothorax, two filaments sometimes arise from a common origin, in which case they are supplied with their tracheæ from the same root (*c*), but these are exceptions to the general structure. The manner in which the sacs are supplied with tracheæ directly from the great trunks of the body, and the distribution of branches of these to the filaments, are important considerations, as the demonstration of these facts fully proves that the sacs in the imago *Pteronarcys* are true respiratory organs. With this object I removed the anterior mesosternal sac from the left side of *Pteronarcys* in connexion with a portion of tegument and of trachea (fig. 3 *a*), and found on examination beneath the microscope that this sac is supplied by a large short branch from the great trunk that passes across the mesosternal surface from the bundle of tracheæ posterior to the prothoracic spiracle, from which bundle other tracheæ pass to the anterior pair of wings, to the œsophagus, and to the dorsal muscles. A precisely similar mode of distribution exists also in the metathorax (fig. 10 *i*, *k*). The division of the trachea within the sac differs a little from what has been described and delineated by M. Pictet * in the larva of *Perla*. In that species the tracheæ are shown to divide abruptly into a multitude of minute ramifications. In *Pteronarcys* the trachea (fig. 4 *b*) divides immediately it enters the root of the branchia into two branches. Each division soon again separates into two, and these again each into two others, and this binary mode of distribution is repeated until the whole terminate in ramifications of similar diameter, one of which enters each branchial filament (fig. 4 *c*), and, gradually becoming smaller from its base to its termination, gives off other small ramifications as it passes onwards, and terminates by dividing into a pair of exceedingly delicate closed tubes. M. Pictet remarks † that he has not been able to satisfy himself in what way the ramifications terminate, and thinks that the interior of these is continuous at their apex with the "*muqueuse interne du tube*," the filament. I am not able to confirm this opinion. On the contrary, I have reason to believe that the terminations, becoming gradually more and more delicate, end as cæca.

Circulation of the Blood.—The blood-corpuscles of the whole body circulate through the branchiæ for the purpose of aëration. The current of blood is always in the vicinity of tracheal vessels, "whether simply along inter-

* *Loc. cit.* p. 87. pl. 3. figs. 3 & 4.

† *Ibid.* p. 88.

cellular spaces," "or bounded by distinct vessels," as I formerly pointed out in my article "INSECTA*," and as since further exemplified by M. Blanchard†. It enters the branchia at the root of the main trachea (fig. 3 *a*) on the anterior or external surface, and, bathing the whole of the branches, penetrates into each filament, passing—as I have repeatedly witnessed in the simple branchiæ of *Sialis*, and I doubt not that the course is precisely similar in *Pteronarcys* (fig. 4)—outwards along the anterior (*d*) and inwards along the posterior surface (*e*), absorbing oxygen, by the principle of endosmose, from the air that is mechanically mixed with the water, and giving out carbonic acid by the same means. This takes place in every form of branchia, so that the function itself, in every structural variety of the organ, is identical, although the conditions under which it is exercised may vary. Thus the broad flattened branchiæ of some of the *Ephemeridæ* may have reference to the occasional detention of blood in those organs under particular circumstances, and a like explanation may account for differences in the form, and in the situation of others.

We have thus established the fact that true branchiæ exist as normal structures in the imago *Pteronarcys*, as well as in the larva and pupa. Now Mr. Barnston has informed me that in both the latter states the insect constantly resides in the water, "at the bottom of streams and rivers;" while the larva of *Perla abnormis*‡, which does not possess the thoracic branchiæ, is always found hidden in the clefts of water-logged timber on the surface, or even in the trunks of trees and other places on the banks,—a difference in habit which corresponds to the difference in structure. The imago *Pteronarcys* is a nocturnal insect; the imago *Perla abnormis* is crepuscular, and perhaps diurnal, although, as Mr. Barnston remarks, "it prefers the shade in the heat of the day." The *Pteronarcys* comes abroad only at dew-fall, or in the night, and Mr. Barnston has observed it, when on the wing, "constantly dipping on the surface of the water." Another able naturalist, Edward Doubleday, Esq., F.L.S., who also has captured the insect in its native haunts, at Trenton Falls, in North America, has informed me, that he has taken it chiefly "on wet evenings," and that it hides itself by day in crevices of rocks which are constantly wetted by the spray of falling water, under stones, and in other damp

* Cyclopædia of Anatomy and Physiology, part xviii. vol. ii. p. 981, 1839.

† Comptes Rendus de l'Institut, May 1847.

‡ See *Perla abnormis*, in the Postscript.

places. This also appears to be the habit of other species of the genus as well as of *Pteronarcys regalis*. Mr. Gosse, who first figured the latter species in his 'Canadian Naturalist,' informs me that he has taken *P. Proteus* and another smaller species in Lower Canada, at Sherbrooke, where the Magog river forms a waterfall of considerable height, on the rocky sides of which, constantly washed by the spray, he has found *P. Proteus* in great numbers, hanging to the sides, or concealed in the crevices of stones and rocks, and that he has but very rarely taken it on the banks of other parts of the river. The *Pteronarcys* thus resembles an amphibious animal in its habit of life, and may be designated,—if I may be allowed the term,—an *Insect Proteus* among the winged *Articulata*,—the representative in structure, as it appears to be in habit, of the *Proteus* of *Vertebrata*. Its organs of respiration fully justify us in instituting this comparison. The true *Proteus* has both lungs and branchiæ, and a similar conformation of structure exists in *Pteronarcys*, in so far as the ramified tracheæ being the direct recipients of atmospheric air, are to be regarded as the representatives of lungs.

Sternal Orifices and Endo-skeleton.—In the short notice which I formerly published on this singular insect*, I pointed out the existence of three pairs of orifices in the tegument of the sternal surface of the thoracic segments (fig. 5 *f*, *g*, *h*), one pair in each segment, between the insertions of the legs, precisely analogous in situation to the respiratory orifices in *Iulus* and some other *Myriapoda*. But as these orifices had not then been traced to their termination within the body, and as their situation in the segments was of doubtful indication in a hexapod insect, no conclusion could be drawn from the mere fact of their existence as to whether they had or had not any communication with the tracheæ. I have now examined them carefully, and find that they pass into the thorax as strong, bone-like tubes, diverging from the axis to the periphery of the body, in the immediate vicinity of some of the principal tracheæ, but that they do not in any way communicate with them, as they terminate abruptly as cæcal structures. They are, in fact, intussuscepted parts of the hardened tegument,—organs of support,—which in most other insects are solid. They are the ento-thoracic portions of the sternal plates in each segment (fig. 14), the *ante-furca* (*u*), *meso-furca* (*v*), and *meta-*

* Annals and Magazine of Natural History, Jan. 1844, p. 23.

furca (*w*), the rudiments of an internal or endo-skeleton, to which the principal muscles of the segments and organs of locomotion, the legs, are attached, and which partially enclose and protect the nervous cord and ganglia, like the rings of vertebræ in the *Vertebrata*. Some traces of the entrances into these furcal bones exist in the sternal plates of *Perla*, but they are flattened and quite unlike those of *Pteronarcys*.

Spiracles.—But although the sternal orifices do not communicate with the respiratory organs, the imago *Pteronarcys* most certainly is endowed with an aërial as well as a branchial form of respiration. It has three pairs of large thoracic spiracles of most complete structure, which are situated in the places usually occupied by these organs in other insects, and which are covered in the pupa of this insect by branchiæ. The first pair (figs. 6, 7, 8) is in the tegument which connects the pro- and mesothorax, the second in the junction of the meso- and metathorax behind the first pair of wings, and the third is in the anterior of the segment immediately behind the metathorax, at the base of the second pair of wings. The segment which bears the latter pair bears also on its under surface a pair of branchiæ, like the true thoracic segments, and ought perhaps to be regarded only as part of the metathorax instead of a distinct segment, the first abdominal. Besides the thoracic spiracles there are also a series of false abdominal ones, one pair at the sides of each segment. These are situated at the precise spot occupied in the second abdominal segment by the last pair of branchiæ (fig. 5 *b*). They are enclosed by a circular elevation in the tegument (fig. 9) and have an imperfect vertical valvular opening, which leads into a small cavity that is closed internally by a cribriform membrane by which the spiracle is separated from the cavity of a large trachea that is connected with it. These spiracles therefore are mediate in structure between the branchial and aërial form of organ, and resemble those which I formerly described in the Transactions of this Society * as common to a genus of *Myriapoda*, the *Heterostoma*. The thoracic spiracles of *Pteronarcys*, on the contrary, are most complete structures. The three pairs are all similar in formation, the second, or mesothoracic, being somewhat the largest. They are placed vertically in the flexible tegument between the segments, and open and shut by a double valve. The pro-

* Vol. xix., Monograph of the Class *Myriapoda*, p. 413.

thoracic spiracle of the left side (fig. 6) has the anterior valve convex, and bounded by a soft, thickened, pad-like, semicircular margin, and resembles the upper lid of the human eye; the posterior valve, on the contrary, has its margin somewhat rigid, is deeply excavated, semilunar, and extended forwards at its superior angle into an elongated, slightly flattened broad process or caruncle, to the posterior border of which is attached a broad levator muscle, which opens or retracts the valve (fig. 8). The inferior angle of this valve has also a small caruncle, which projects slightly over the anterior valve when the spiracle is completely closed, but which has almost disappeared when the spiracle is expanded. The closing of the spiracle seems to be effected by circular fibres in the tegument, very similar to those of the orbicular muscle of the eye in *Vertebrata*, attached (as shown in fig. 7) at the anterior superior angle. The closure of the spiracle is completed (as in fig. 6) by the action of other muscles on the tegument behind the posterior valve, by which this is carried forwards, and its process is made to cover and shut down like a lid on the anterior valve, so as to render it impossible for anything to penetrate into the chamber of the spiracle when the valves are completely closed. This structure indicates that the action of these respiratory orifices is under the control of the will or instinct of the insect, as well as of the reflected influence of the nervous power on the application of stimuli, and probably has some direct reference to the habits of this anomalous insect.

But what peculiar modification in œconomy can we infer from this duality of respiratory organs, branchiæ and spiracles in the same individual? Can it be that the imago *Pteronarcys* ever actually re-enters the water for any purpose after it leaves it, as Mr. Barnston has informed me it does, to change to an imago under stones, on the banks of rivers? Does it ever as a perfect insect dive in search of food? or, besides residing constantly in the most damp situations, does the female, creeping down the stems of water-plants, as is said to be the habit of *Phryganea grandis**, descend beneath the surface of the stream to deposit her ova, or the male to assist in her operations? These are questions which only a close attention to the habits of the insect can solve, whilst the duality and the peculiar structure of its respiratory organs admit of their being entertained. That the structure of the spiracle may have refer-

* Curtis, British Entom., fol. 592.

ence to a frequent submersion of the insect may fairly be inferred from facts supplied to us by comparative anatomy in the *Vertebrata*. The nostril of the common Seal has a form somewhat analogous to that of the spiracle of this insect, which the animal closes most effectually, at will, when he dives, and a similar power may be possessed by *Pteronarcys* and its affinities.

Distribution of the Tracheæ.—The internal organs of respiration are almost as remarkable in their distribution and structure as the external. In most winged insects, more especially those of swift flight, or with large wings, the principal tracheæ of the body are either considerably enlarged in diameter, or are dilated in some parts of their course into vesicles or sacs. But although *Pteronarcys* has large and powerful wings, its flight is laboured, heavy and slow, while not a trace of vesicular structure exists in any part of its internal respiratory organs. Even in the principal tracheæ of the thorax (fig. 10 *i*, *k*), which communicate directly with the spiracles by small chambers, from which go off the main trunks to the wings, to the dorsal and ventral surfaces, and to the alimentary canal, there is only a very slight enlargement. In other parts of the body the tracheæ are uniform in size, are narrow, slender, and ramose. They are of a light brown colour, as in *Perla*, and differ in this respect from those of *Sialis*, which are of a jet-black. The principal trunks at the sides of the segments consist of two sets, which pass backwards, curved in opposite directions, from one segment to another, like the abdominal tracheæ in *Melolontha*, as shown by Strauss *, and as I have found also in *Lampyris* and some other genera. These trunks unite opposite to each spiracle, and then divide and pass on to the next and are again united. They are smaller in diameter, compared with the size of the insect, than the corresponding tracheæ in *Sialis*, or even in *Perla*. In each of these genera, as in *Pteronarcys*, the respiratory system is without vesicles, although in *Sialis*, which is slow and heavy in flight, the principal tracheæ are somewhat enlarged. The largest tracheæ in each of these genera are the lateral and transverse trunks of the sides and pectoral surface of the thoracic segments. Besides these, there are in *Pteronarcys* and *Perla* a pair of longitudinal tracheæ, passing directly backwards on each side of the nervous cord and gan-

* Considérations générales sur l'Anatomie Comparée des Animaux Articules, &c., 1828, 4to, pl. 7. fig. 4.

glia, which are somewhat larger than corresponding tracheæ in other insects in which the lateral abdominal trunks are dilated into sacs. A curious termination of the lateral abdominal trunks occurs in the posterior segments. These trunks end abruptly immediately after their junction (fig. 11) in a kind of cæcum, from which a small branch extends backwards to the caudal styles, analogous to the mode in which the branchial filaments are supplied from the main tracheæ. One of the most curious distributions of tracheæ in *Pteronarcys* is of those which are supplied to the alimentary canal. Tracheæ which supply this organ are rarely or ever dilated in any insect, not even in the *Hymenoptera*, in which the sacs of the main trunks are the largest. They pass off as slender branches, either from the lateral sacs or from the main trunks in the immediate vicinity of the spiracles, and decrease in size as they are distributed on the canal, as I have figured and described* in the male of *Bombus terrestris*. A slender branch passes longitudinally backwards in that insect from the main trachea, behind the metathoracic spiracle on each side of the œsophagus, to the anterior portion of the stomach on which it is distributed, and a similar origin and distribution of the gastric tracheæ exists in all insects with but little variation. In *Pteronarcys* a long, slender branch (fig. 10 *i*, *k*) passes off from the slightly enlarged trunk behind the mesothoracic spiracle, and another (*l*) from behind the metathoracic, which are extended longitudinally backwards, slightly reduced in size, as far as the middle of the abdomen, where they divide into branches which are distributed on the sides and anterior of the stomach. This is the general character of the tracheæ in the whole of the *Perlidæ* and in *Sialis*. These exceptions to the law which I have heretofore endeavoured to exemplify by facts, that a vesicular form of the respiratory organs in insects has reference chiefly to power of flight, and enables the insect to alter the specific gravity of its body at the moment it takes wing, and thus diminish the amount of muscular exertion required in its movements, tend in reality to confirm the previous conclusions. The retention in the imago of the simple setaceous tracheæ of the larva is accompanied, as in *Sialis*, *Perla*, and *Pteronarcys*, with a low power of flight, although the species of each of these genera have ample wings, and might have been expected to be extremely active. *Pteronarcys* thus resembles

* Philosophical Transactions, 1836, part ii. pl. 26. fig. 2. p. 564.

Perla and *Sialis* in the general character of its respiratory organs, but it differs from them in other parts of its structure.

Alimentary Canal.—The *alimentary canal* (fig. 10) consists in chief part of an enormously elongated œsophagus (*m*), which, instead of joining with the stomach (*p*) in the metathorax, passes backwards, accompanied by the tracheæ (*k*, *l*), as far as the fourth segment of the abdomen, and then terminates in the digestive organ, which does not exhibit even the smallest rudiments of gastric glands, which exist of large size in *Perla* (fig. 12 *o*). This proves as marked a difference in the habits of these two genera as exists between these and *Sialis* (fig. 13), in which the œsophagus is extended backwards in the form of a pouch (*n*), as in the Diurnal *Lepidoptera*. The stomach (*p*) of *Pteronarcys* differs as much from that of *Perla* as the œsophagus. It is capacious, muscular, and of considerable length, forming two or three convolutions before it terminates in a pylorus, around which the Malpighian vessels are inserted; whilst that of *Perla abnormis* is surrounded at its cardiac origin by six large cæcal glands (*o*), is short, somewhat funnel-shaped, straight, and has no convolution. In these respects the stomach of *Perla* resembles that of the *Blattidæ*. In the number, appearance, size, and place of insertion of the Malpighian vessels (*r*), *Pteronarcys* resembles *Perla*, but both differ from *Sialis*, in which there are only six of these vessels, while in the others there are from forty to fifty. These three genera also differ as regards the ilium (*q*), and the form and size of the colon (*s*). In *Pteronarcys* and *Sialis* the ilium is short and slender, but it is more than twice as long in *Perla*. The colon in the latter is very muscular, is almost as large as the stomach itself, and has a cæcum projecting from it. In *Sialis* the colon is larger than the stomach, and has a small lobulated cæcum at its commencement, as in Lepidopterous larvæ; but in *Pteronarcys* it is shorter and much smaller than in either of these genera. These differences in organization indicate differences in kind of food, or in habit and œconomy, and establish the distinctness of the genera. The existence of gastric glands in *Perla* shows that this genus stands at the head of its family, and approaches the *Orthoptera*; while the absence of these in *Pteronarcys*, and in the smaller *Perlidæ*, *Nemoura*, shows also that these genera are of a type inferior to *Perla*.

Nervous System.—The nervous system of *Pteronarcys* (fig. 14) leads us to a

conclusion similar to that which we arrive at from the anatomy of the digestive organs. The number of segments to the body in *Pteronarcys* and *Perla* is the same, fourteen in each, but that of the ganglia of the nervous cord is different. In *Pteronarcys* the nervous system is composed of the brain and cord with twelve subœsophageal ganglia. The first of these, the analogue of the *medulla oblongata* of *Vertebrata*, is situated, as in other insects, in the head, immediately below the brain, or cephalic ganglia, and supplies the organs of manducation, the mouth and pharynx. The second, third and fourth, of larger size, are in the three segments of the thorax, one in each, supplying the organs of locomotion, the legs and wings; and eight smaller ganglia, the first of which is in the metathorax, at a short distance behind the great ganglion of that segment, while the remaining seven are in the abdomen. But the nervous system in *Perla* consists of the brain and only ten ganglia in the cord. Of these the *medulla oblongata* and thoracic ganglia are in their usual situation, but the meso- and meta-thoracic are larger than in *Pteronarcys*, more especially the latter, owing to the fifth, or first of the smaller ganglia of the cord, having united with the metathoracic in *Perla*, during the changes of the larva and pupa, as I have elsewhere shown * takes place also in the metamorphoses of the *Lepidoptera*, together with a shortening of the cord in one or more of the basal segments of the abdomen. Owing also to a similar cause, the shortening of the interganglionic portion of cord, the analogue of the sixth ganglion in *Pteronarcys* occupies the position of the fifth of that genus in *Perla*, the sulcus of the metafurca (*w*); while the seventh of *Pteronarcys* is situated in *Perla* at the anterior of the basal segment of the abdomen, and is separated from the preceding ganglion only by a very short portion of cord. Similar alteration in position, with coalescence of ganglia, seems to have taken place at the termination of the cord in *Perla*, in which the eleventh and twelfth ganglia of *Pteronarcys* seem to have become united. This may account for the remarkable difference in the number of ganglia in these two genera. *Perla* is thus as much in advance of *Pteronarcys* in the general structure of its nervous system, as in that of its digestive and respiratory organs. Approaching as these two genera do in their entire organization to the *Orthoptera*, they seem to represent some of the lower forms of the

* Philosophical Transactions, 1834, part ii.

perfect and larva states of insects of that Order. *Perla*, with its enlarged tracheæ, its sacculated stomach and colon, and its more concentrated nervous system, is much in advance of *Pteronarcys*, which retains the larva type of organization in all its structures, branchial organs of respiration, a capacious œsophagus and elongated alimentary canal, and more numerous and separated ganglia in its nervous cord. On passing from the general conformation to the details of its nervous system, *Pteronarcys* still preserves the same inferiority. The *cephalic ganglia*, which constitute the brain, have not completely coalesced, as in some of the more perfect insects, but have only partially united in the middle line above the œsophagus; while the antennal ganglia in front of them are also distinct and separate. The *ocelli* on the front and vertex of the head in the perfect insect (fig. 10) are supplied by short nervous trunks, which proceed directly from the cephalic ganglia (fig. 11). The anterior or median ocellus is primarily a double organ. It derives its nerve from two trunks, which originate one from the front of each of the cephalic ganglia, and which immediately are united laterally to form the nerve to the ocellus. This is the mode of origin of the anterior ocellar nerve in *Pteronarcys*, as I have found it to be also in *Hymenoptera*, and other insects. The posterior ocelli are supplied each by single trunks from the two cephalic ganglia. The true optic nerves, which supply the compound lateral eyes of the insect, have distinct gangliform enlargements at their base, and are expanded at their termination into a broad retina.

The *nervous cord* exhibits distinct indications of its compound structure. The aganglionic portion, which I formerly described * in *Lepidoptera*, is very distinctly seen on its superior or visceral surface, while passing over the ganglia in the thoracic segments (*u*, *v*, *w*). It gives off a branch on each side in its course between the pro- and meso-thoracic ganglia in company with some organic or transverse fibres. This branch passes diagonally backwards, distributes some ramifications to the respiratory organs connected with the prothoracic spiracle, and then joins the first nerve from the meso-thoracic ganglion, and with it forms the anterior *alar* nerve that supplies the muscles of the first pair of wings, thus directly associating the function of respiration with that of flight. The origination of the wings, during

* Phil. Trans. 1834.

the changes of the insect, in a fold of tegument that includes branches of tracheæ, is thus in most perfect harmony with the character of the nerves that regulate their mixed functions. The cord also gives off, between the meso- and meta-thoracic ganglia, another compound branch, which first supplies the second or mesothoracic spiracle and tracheæ, and then unites with the first nerve from the metathoracic ganglion, to form the *second alar nerve* to the muscles of the second pair of wings. Besides the posterior, or ganglionic roots of the alar nerves, each ganglion gives off two others, one small one to the muscles of the segment, and another, the largest nerve of each ganglion in *Pteronarcys* and other *Perlidæ*, to the legs. In all insects of powerful flight, the *alar* are the largest nerves of the trunk; but in insects of inferior power of wing, as in the *Perlidæ*, and more especially in those in which the legs are strong and much employed, the *pedal* nerves, as in *Pteronarcys*, are much the largest.

The aganglionic tract of the cord is as distinct in its transit over the ganglia in the abdominal region as in the thorax. Each ganglion gives off a large trunk to the muscles of the segment, and anterior to each, lying loosely upon the aganglionic tract, a nerve passes off on each side to the false spiracles and internal organs of respiration. These are the *transverse* or *respiratory* nerves, which I formerly described * in the larva of the *Sphinx*, and which in perfect insects usually become approximated to, and most closely connected with, the trunks from the ganglia. They are the analogues of the compound anterior roots of the *alar nerves*. Some of them have not united with the other trunks in the anterior segments of *Pteronarcys*, but remain as in the larvæ of *Lepidoptera*, thus further indicating the low type of development in this genus. Others, although they have joined with the ganglionic trunks, present irregularities in their position and distribution. The terminal ganglion of the cord, as in other insects, supplies the organs of reproduction and the terminations of the alimentary canal.

Organs of Reproduction.—The organs of reproduction in *Pteronarcys* are formed on the same inferior type as those of other parts of its system. They differ less from those of *Perla* than its other structures. The specimen I have dissected proved on examination to be a male, and showed that a curious

* Phil. Trans. 1832 and 1834.

error has been committed by M. Pictet in regard to the sexes of *Pteronarcys*, as I shall presently show.

The male internal organs are very simple in their character. They consist of a pair of *testes* (fig. 14 *x*) with long convoluted ducts, and a pair of short *vesiculæ seminales* (*y*). These, with the ducts, unite behind the terminal ganglion of the nervous cord in a short *vas deferens* on each side, which terminates in a long *ductus ejaculatorius* and organ of intromission (*z*).

The *testes* are placed above and on each side of the alimentary canal in the fifth, sixth and seventh segments of the abdomen. Each testis (*x*) is formed of a multitude of pear-shaped follicles attached around, and opening into a common canal. These follicles (fig. 15) are filled with rounded bodies, which line their interior, the proper secretory structures for the production of spermatozoal cells, some of which, of minute size, I have observed at the junction of the follicles with the canal. The aggregation of follicles together forms an elongated oval testis, which terminates in a long convoluted duct. The *vesiculæ seminales* (*y*) are short, thick cæcal organs of an opake white colour, and folded twice or thrice on themselves. They occupy the posterior part of the eighth abdominal segment, and are continuous backwards with the *vasa deferentia* on each side, at the point of union of the ducts from the testes. The *vasa deferentia* thus formed pass backwards to the margin of the eighth abdominal segment, and then unite laterally and pass to some distance forwards, where they end in a single vessel, a long *ductus ejaculatorius*, which returns backwards to the outlet of the tenth segment to end in the penis (*z*). The object of the great length of this duct, and of the arrangement of the organs, seems to be to facilitate the transmission of the male influence at the time of union of the sexes. The long process on the under surface of the eighth segment (fig. 16) appears to be elevated and employed by the male as an organ of prehension, to grasp and retain the terminal segment of the female, the body of the male being reversed during the act, as in the *Dermaptera* and *Orthoptera*. By the elevation of the process of the eighth segment, and the elongation of the ninth and tenth segments, the position of the *vesiculæ* and *ductus ejaculatorius* is altered, and the passage of the male influence is then direct and unimpeded.

M. Pictet, however, has mistaken the process in the male for an ovipositor,

and consequently has described the male *Pteronarcys* as the female, and the latter as the male. He seems to have been led into this very error, which he points out as having been committed by others *, by confining his attention chiefly to *Perla*, in which he correctly says that the reproductive organs "in the males open at the extremity of the abdomen, whilst in the females the entrance of the oviduct is under the eighth ring." This description is perfectly true, as a matter of fact, both in *Perla* and *Pteronarcys*. Nevertheless, M. Pictet has confounded the sexes of the latter, by mistaking the prehensile appendage of the male for a supposed ovipositor of the female, which does not possess such an organ, but in which the outlet of the oviduct is situated in the eighth segment, precisely as in *Perla*, as I have found on examination of specimens of this sex of *Pteronarcys regalis* (fig. 17) now in the cabinets of the British Museum.

The body of the female *P. regalis* (fig. 17), and of other species of this genus, is easily distinguished from that of the male. The segments are more depressed, are much broader than long, and altogether are less elegant in form. The terminal tenth segment is considerably wider than in the male, and is only partially divided longitudinally on the under surface into two valves, each of which is marked with an imperforate spiracle, the situation of the caudal branchiæ in the larva. The valves are united at their base, and are separated throughout the remainder of their length only by a slight sulcus. The female organs open externally in the eighth segment (fig. 17. 8), which has its ventral surface divided longitudinally into two plates, which cover the entrance to the oviduct. The margin of the segment, in some specimens, is simply notched in the middle, at the point of junction of the plates, as in the one delineated; but in others there are two minute processes at the angles of the notch, the rudimentary representatives of corresponding, more elongated parts in the male, which, united, form the process of the eighth segment (fig. 16. 8). These parts, which are of their smallest size in the females of this, are much larger in those of other species. In the original specimen of *P. biloba*, now in the British Museum, and correctly regarded by Mr. Newman as a female, not only the margin, but a large part of each plate is included in two triangular curved lobes, from which the species is named.

* *Loc. cit.* p. 37.

The male of this species, in which we may expect to find these parts much more developed, is unknown. The female of a third species, *P. Proteus*, differs both from *P. regalis* and *P. biloba*. Instead of having the margin of the eighth segment notched, it has it slightly elongated and rounded in the middle, and it is not divided longitudinally into two plates. In this respect it somewhat resembles the male *P. regalis*. It is thus evident that the mere presence or absence of a process to the eighth segment is not a character peculiar to either sex; as a rounded margin to this segment exists in some *Perlæ*, as well as in *Pteronarcys Proteus*. The distinctive character of the sexes in *Pteronarcys* is the *length* of the process. The notched or toothed margin in the female *P. regalis* is elongated into a bifid appendage in the male; whilst the slightly developed part in the former sex of *P. Proteus* also is enlarged into a long, thick, spoon-shaped structure in the latter, very different in shape from the corresponding part in the same sex of *P. regalis*. The view entertained by M. Pictet, that the appendage to the eighth segment is characteristic of the female *Pteronarcys*, and that it is designed for the purpose of retaining her eggs, thus appears to be incorrect as regards this genus. Nevertheless, it may be valid as regards *Perla*, in which the structure is absent in the male. Scopoli *, Suckow †, and Curtis have remarked that the female *Perla cephalotes* carries her eggs in a mass, inclosed in a membrane, at the apex of the abdomen; and there is a specimen of *Perla abnormis* in the collection of the British Museum, taken by Mr. Barnston in Canada, which has a rounded mass of small black eggs attached to the eighth segment, like the egg-capsule in *Blatta*. Another observer, Mr. Westwood ‡, has noticed a similar mass of eggs borne by a female *Eusthenia diversipes*. Thus the view is correct as regards *Perla* and *Eusthenia*, although quite unsupported with reference to *Pteronarcys*. The female of *Perla abnormis* has the whole margin of the segment semicircular, and it is deeply incised in a diagonal direction on each side, so as to form a kind of lid or valve, from behind which the eggs in Mr. Barnston's specimen project §. The males

* Ent. Carniol. p. 705. † Zeitschr. Organ. Phys. t. ii. No. 3. Mar. 1828.

‡ Introduction, &c. vol. ii. p. 22.

§ M. Pictet seems to have noticed a somewhat similar shield-shaped process in the females of *Perla Hanii* (pl. 19. figs. 10 & 11) and *Perla limbata*.

of this species, of which I have dissected several, have not the slightest rudiment of process from the eighth segment, nor any enlargement of its margin.

These marked differences of structure in the external organs of reproduction still further distinguish *Perla* and *Pteronarcys*, and seem to indicate that there are some differences of habit on the part of the females with regard to their oviposition. Of the internal anatomy of the female I can only speak generally, as I have not been able to procure a specimen sufficiently good for precise description. The only one I have dissected had originally been preserved in a dried state. It may, nevertheless, be of use to compare the few facts I have noticed in the anatomy of *Pteronarcys* with those of *Perla*, more especially as the internal reproductive organs have not yet been described in the former of these genera. The general structure in both is similar, and that of the organs in the two sexes differs less than in most other insects. In *Perla* as in *Pteronarcys* the follicular testis of the male (fig. 14 *x*) is represented by a multitude of short ovigerous tubes, which, aggregated together around and opening into a common duct or cavity, constitute the ovary in the female. Each egg-tube, of which there are upwards of twenty in each ovary, is filled with at least ten distinct rudimentary ova, which give it a beaded or nodulated appearance. It is large and dilated at its base, and is rapidly diminished in size in proportion to the distance of its attachment around the egg-chamber of the duct. It is the representative of the short cæcal follicle (fig. 15) in which the spermatozoal cells are formed in the male, and which, instead of being arrested at the follicular stage of development, continues to be elongated, while some of the nuclei of its centripetal layers of cells, in which the forces of growth are most energetic, become individualized as separate organisms, the germs of future ova, and which, more rapidly nourished by the principle of endosmose than the surrounding cells, constitute the materials of future beings. In like manner the convoluted spermatic duct of the male (*x*, *y*) is represented by a long dilated oviduct, which commences in the egg-chamber, in the female, and which differs but little, except in diameter, from the spermatic or deferential duct of the male; and, like it, terminates, by junction with its fellow of the opposite side, in a common passage for the eggs, the analogue of the ejaculatory

duct (*z*) formed by the union of the deferential ducts of the two sides and of the seminal vesicles. At the point of union of the analogues of these parts in the female the passage is dilated into a large cæcal cavity, from the closed end of which, on each side, proceed two diminutive cæca, the undeveloped representatives of the *vesiculæ seminales* (*x*) of the male. The dilated pouch-like cavity in the female, the so-called *spermatheca*, which receives and retains the influence of the male at the union of the sexes, is thus an enlarged uteroid expansion of a portion of the common oviduct which is formed by the union of the terminations of the deferential and seminal tubes of the male. This is the general anatomy of these organs, both in *Pteronarcys* and *Perla*; and to which that of all other Hexapods, subject to variations in the relative development of particular portions of these structures, is conformable.

From this comparative examination of structure in *Pteronarcys* it may be asked, what are the proper affinities of the insects of this genus? and whether, with the other *Perlidæ*, they occupy a proper position in the arrangement of systematists? The great similarity of the digestive organs of *Perla* to those of the *Blattidæ*, and the remarkable existence of certain talc-like structures on the head in insects of this family external to the ocelli (fig. 10), resembling others which are known to exist at the base of the antennæ in the *Blattidæ*, suggest the conclusion that if the *Megaloptera*, including *Perla* and *Pteronarcys*, are not joined to the *Orthoptera*, they ought at least to follow that Order, at the head of the *Neuroptera*, and to be succeeded by the *Libellulæ*, *Agrionidæ* and *Ephemeridæ*, as the most natural arrangement, and as most conformable to their anatomy.